TITLE: FOOD COMPETITION IN A SEMIFREE-RANGING *Cebus apella* GROUP

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ABSTRACT

The competitive regime faced by individuals is fundamental to modelling the evolution of social organisation. In this paper, we assess the relative importance of contest and scramble food competition on the social dynamics of a provisioned semifree-ranging *Cebus apella* group (n= 18). Individuals competed directly for provisioned and clumped foods. Effects of indirect competition were apparent with individuals foraging in different areas and with increased group dispersion during periods of low food abundance. We suggest that both forms of competition can act simultaneously and to some extent synergistically in their influence on social dynamics; the combination of social and ecological opportunities for competition and how those opportunities are exploited both influence the nature of the relationships within social groups of primates as well as underlying the evolved social structure.

INTRODUCTION

The distinction between contest (or direct) and scramble (or indirect) competition is fundamental to modeling the evolution of social organization (Isbell, 1991; van Hooff & van Schaik, 1992; Sterck *et al.*, 1997; Isbell *et al*, 1998; Isbell & Young, 2002; Boinski *et al.*, 2000). In addition, ecological constraints are important factors shaping social interactions. When food is found in clumped or usurpable patches, the benefits of contest competition outweigh the costs of potential wounds or energy expenditure resulting from aggressive interactions. In these cases, where direct competition prevails, the establishment of linear dominance hierarchies is predicted, and coalitions are expected between group members if foods can be shared among coalitionary partners (Sterck *et al.*, 1997; Boinski *et al.*, 2000; Isbell & Young, 2002). When indirect competition prevails, as in the absence of clumped resources, groups are thought to form more egalitarian or unstable hierarchical relationships, and coalitions are thought to be rare or irrelevant to the dynamics of food competition, although coalitions may form for reasons such as access to reproductive or other socially valuable partners (Sterck *et al.*, 1997; Boinski *et al.*, 2000; Isbell & Young, 2002).

Analyses relating proximate ecological conditions to the nature of social groups, and to social interactions and behavioral patterns within these groups contribute to developing socio-ecological models. However, while behavior indicative of contest competition is readily observable, e.g. overt aggressive conflicts associated with food and those associated with hierarchical maintenance (Janson & van Schaik, 1988; Sterck *et al.*, 1997), the behavioral manifestations of scramble competition are harder to distinguish. Suggestive short term indicators of scramble competition are: a) increases in home-range and/or day-range size (e.g. larger groups needing larger home ranges, or increases in day

ranges during periods of food scarcity (Isbell *et al.*, 1998) and b) decreased cohesiveness among individuals in groups facing heightened competition (White & Chapman, 1994) or during periods of food scarcity (Dunbar, 1988). Lower fertility in larger groups (Oates, 1987) may be regarded as a longer term consequence of scramble competition, although not a behavioral one.

In wild capuchin monkeys (genus *Cebus*), both contest and scramble competition occur. For *Cebus capucinus*, aggression was less frequent when individuals foraged in dispersed patches than when foraging in clumped food resources (Phillips, 1995a, b; see also Vogel & Janson, 2007). In *C. apella*, overt contests over clumped feeding sites resulted in the establishment of a linear hierarchy, such that dominant individuals had a four-fold increase in food intake over that of subordinate members when foraging in preferred fruit trees. As a result, dominants had a significantly greater total energy intake, particularly during the dry season (Janson, 1985).

Scramble competition in *Cebus* groups is indicated by a decrease in time devoted to social activities in groups inhabiting poorer habitats relative to those inhabiting richer habitats (Rose, 1994). In periods of low food abundance diets shift to lower quality but more abundant resources; groups minimize the risks of starvation in periods of low food abundance by having a larger home range and using it as a function of the abundance of fruit trees in different periods (Robinson, 1986; Galetti & Pedroni, 1994). In *C. olivaceous* and *C. apella*, individuals in larger groups spend more time foraging, have a longer daily travel distance and a tendency to spend more time in both grooming and aggression (de Ruiter, 1986; Janson, 1988; Izar, 2004).

The combined importance of contest and scramble competition in the social dynamics of capuchins is suggested by the relationship between rank and the positioning of the individuals during their daily activities. Non-random positioning typifies capuchin

groups (Robinson, 1981; Janson, 1990a, b; Hall & Fedigan, 1997) and influences the foraging success of individuals: the best foraging positions (front-center) are occupied by the alpha male and female, higher predation risk positions (periphery) are occupied by subordinate adults and safer positions (center) by juveniles. It remains unclear whether these positions are the outcome of receiving aggression (Janson, 1990b), of the active avoidance of dominants (Hall & Fedigan, 1997), of the alpha's tolerance of immatures (Robinson, 1981), or of an interaction with opportunities for contest as noted by Vogel & Janson (2007). The relations between food competition and positioning patterns are not yet clear and these vary by species and ecological characteristics of the study area.

Boinski *et al.* (2000) argued against the use of results collected from populations under conditions of "natural experiments" to evaluate socio-ecological models because many atypical factors influence the social dynamics of such groups. Notwithstanding this caveat, for both natural and "behaviorally altered or disturbed" groups (provisioned or semifree-ranging), a major issue is not the atypical influences on behavior but rather a consistent difficulty in defining the social consequences of either type of competitive regime.

We aim to explore the influence of provisioning, if any, on the competitive regimes exhibited within a semifree-ranging brown capuchin (*Cebus apella*) group. Specifically, we aim to assess whether provisioning buffers individuals against energy shortfalls, such that manifestations of feeding competition are rare, or whether provisioning enhances opportunities for competition. Thus, we emphasize the importance of all agonistic interactions as mechanisms to both gain access to resources and to structure hierarchies and underlie competitive success.

Two predictions are tested:

1. If individuals contest over food items which may be both monopolizable and preferred, then aggressive behaviours will increase with the use of clumped provisioned resources. As the provisioning is distributed during the midday period, we would expect an increase in aggressive events during this relative to other period of the day.
2. If scramble competition occurs, then the extent of the area used by individuals and group cohesiveness will vary between periods of high and low natural food abundance (i.e from wet to dry seasons), irrespective of provisioning.

Aspects of contest and scramble competition are distinguished using seasonal variation in activities and in overall agonistic interactions, location within the habitat (ranging) and cohesiveness among group members. Variation in daily patterns of interaction (e.g. that associated with provisioning) and between seasons are controlled for in the analyses. In addition, if these aspects of competition are general across group members, we expect to find similarities across the age-sex classes. These behavioral predictions are expected to produce a pattern of non-random spatial structure (e.g. Janson, 1990 a, b), which can act as the basis for variance in social organization with ultimate consequences for the evolution of social systems (Sterck *et al*., 1997).

METHODS

Study Group and Study Site

The study group consisted of 20 individuals (3 adult males, 4 adult females, 2 subadult males, 6 juvenile males, 3 juvenile females and 2 infants). There was one clear alpha male, an alpha female and an age-size based hierarchy for the rest of the group (Ferreira, 2003; Izar *et al*., 2006).

The study group was semifree-ranging in what was effectively an island of reforested area of 18ha within the Tietê Ecological Park (total area of 1400 ha in eastern São Paulo State, Brazil). Despite the absence of large predators of *Cebus* (eagles, cats or boa constrictors; Izar, 1994) in this area, dispersal was difficult due to extremely low food abundance in the surrounding area. The group was provisioned daily with five maize cobs, 36 bananas, 2 papayas, 10 apples and 8 oranges (approx 5300 kcals total; USDA National nutrient database: www.nal.usda.gov/fnic/foodcomp), and provisioned food was distributed at midday on a circular platform of one-meter diameter. Provisioned foods were of high quality, large (half banana, half apple, half maize cob, half orange, 1/6 papaya), readily monopolizable, but estimated to be sufficient to meet only approximately half of average daily energy requirements of the animals (using total mean body mass and equations for calculating ADMR; e.g. Ulijaszek & Strickland, 1993); as a result the monkeys also foraged for natural foods.

Two distinct seasons were defined: one wet and warmer (October to March, mean monthly rainfall of 178 mm; average temperature 19-24ºC) and one dry and cooler (April to September, mean monthly rainfall of 69 mm, average temperature 15-17ºC). Day length ranges from a maximum of 13 hours (5:30 am to 6:30 pm) in the wet-warm season to 11 hours (6:30 am to 5:30 pm) in the dry-cool season.

Data Collection

From October 1999 to June 2001, the group was accompanied by an observer (RGF) for 867 hours. The data used here derive solely from the period after full habituation of the animals, from Jan 2000 to Jun 2001, but includes a 20-day period of social instability caused by the death of the group's original alpha female. There was a total of 492 hours of contact over two dry and two wet seasons, during which data on events of aggression,

coalitions and grooming were collected on an all-occurrences continuous record basis. These data consisted of initiator, recipient, actions and reactions and assumed that there were no systematic biases due to differential visibility. Focal animal data totaling 304 hours was collected on individuals observed for a period of 10 minutes, five times each month using a random order of observation of different individuals each day. During each focal scan sample the activity, the identity of their nearest neighbor, and animals spatial position relative to other group members (central, peripheral, front, rear) for all behavioral categories were recorded every minute, while location within the reserve was recorded only once within the observation period (see below).

Behaviour recorded on each minute of the focal sample ('scans') was classified into six mutually exclusive activity categories; 1) Foraging: visually searching, procuring, manipulating (including tool use) and ingesting foods. 2) Rest. 3) Locomotion (movement in any direction). 4) Groom (groom other or be groomed). 5) Agonistic interactions which included: a) high intensity aggression (chases, pushes and bites), b) avoidance behaviour (retreats, flees), c) threats and d) signals of submission. 6) Social play. Other activities such as scratching and interacting with other species were excluded from consideration here as they represented only 1.6% and 1.1% of all focal observations respectively. Such activities tended to occur as rapid events within behavioural states. During focal samples, participants, direction and outcome of interactions were also recorded on a continuous basis. Although activities were sampled on a minute by minute basis from individuals, location data at longer intervals were used to determine how the group used the space within the study area.

The study site (18 ha) was divided in sub-areas based on special features of the environment (e.g. buildings, large trees, and lakes). The sub-area where the focal animal was observed for *at least* 5 min was assigned as one home range point for that sample.

Point samples were taken to represent group location since samples with no other individual within a 10m radius of the focal for more than 5 min were excluded.

The number of location samples was compared among three areas of the range which differed in mechanisms of food acquisition:

1. Area 1 which included a veterinary clinic, the kitchen or food preparation area, and an area of approximately 30 m to the right and back of the kitchen. This area was poor in plant diversity with only a corridor of *Hibiscus sp* and some orange trees. However, the animals frequently stole food from the kitchen and the trash bins located around the buildings, offering limited opportunities for monopolization and contest competition.
2. Area 2 had a variety of plant species including natural food trees, *Siagrus romanzoffiana* and some *Nesperina sp*. This area contained one cage with callitrichids (*Callithrix jacchus*) and one with a peccary (*Tayassu albirostris*), and the capuchins constantly stole food from both cages. In addition and most importantly, Area 2 had the platform where the daily food ration was distributed. This area of provisioning and other species' food offered major opportunities for monopolization and contest competition.
3. Area 3 was larger, with a greater natural plant density and abundance. Animals had to actively search to obtain food, and opportunities for monopolization of discrete food patches were infrequent.

The number of individuals in a radius of 10m of the focal subject, recorded every minute in focal samples, was used as an indicator of cohesiveness. The number of scans (point samples) where only the focal individual was present in a radius of 10m was compared with the number with three or more individuals present within 10m. These individual totals were summed across all focal samples, and no individual contributed

disproportionately to the overall totals. While successive records of nearest neighbors can often be autocorrelated within the same focal-scan sample, the use of five bouts of 10 minutes scan samples per months diminishes the problem of time dependency on cohesiveness values. Thus although hierarchical dominance and affiliative relationships may influence proximity between individuals, this individually-derived measure of "many" versus "few" neighbors was used to describe cohesiveness. Scans with only mother-infant dyads present were excluded from analyses since these dyads could bias the analysis of group cohesiveness.

Figure 1 about here

Statistical Analyses

Due to potential effects of energy buffering due to lactation, infants were excluded from all analyses. The two subadult individuals were considered as adults in analyses. Comparisons between ages and sexes were made within each season and limited to two categories: male *versus* female and adult *versus* juvenile.

Food was distributed to the monkeys at around midday. Thus interactions and activities would be expected to differ by time of day if there was contest competition over provisioned items. In order to account for differences in the total number of focal samples on each individual and in different periods of the day (two focals from 0600-1059, two from 1100-1459 and one from 1500-1900 on each individual every month), data were normalized according to the following formula:

$$x' = \frac{\left(x_m \times F_a / F_m\right) + \left(x_{mi} \times F_a / F_{mi}\right) + x_a}{F_a \times 3}$$

where: x' is the proportion of behaviour x for one individual; x_m is the total of scans where that individual performed behaviour x during the morning period; x_{mi} is the total of scans where that individual performed behaviour x during the midday period; x_a is the total of

scans where that individual performed behaviour x during the afternoon period; F_m is the total of scans on this individual during the morning period; F_{mi} is the total of scans on this individual during the midday period and F_a is the total of scans on this individual during the afternoon period. The formula was used because individuals had different numbers of good observations within each month.

Age-sex and seasonal comparisons of activity budgets were made on individuals. Data were tested for normality; when normal, parametric ANOVA (F) and t-student test (T) were used. Otherwise, non-parametric Kruskal-Wallis (U) and Wilcoxon Matched Pairs Signed Ranks (Z) were used for comparisons among states and between conditions. Correlation (Spearman r_s) and Chi-square (χ^2) analyses were performed to explore associations between activities, to compare frequencies of the use of areas, and to test whether cohesiveness was greater during wet than during dry periods, respectively. As with any behavioural study with limited numbers of individuals and observations, the power of statistical tests will be low; however, we report effect sizes which at $p \leq 0.05$, two tailed, are likely to be robust.

RESULTS

Seasonal and diurnal variations in behaviors

Foraging constituted the most frequent activity accounting for 55 to 60% of an individual's time in both seasons (Wet: mean 53.9% ± 2.6, Dry: 58.4% ± 2.2; N=18; t-test T = 1.9, *NS*), while grooming occupied only a minor fraction (Wet: Median = 0.6, inter-quartile range IQR = 2.9; Dry: 1.1, IQR = 2.9, N=18, Z = 0.7, *NS*) of an individual's activity budget in both seasons (Figure 2).

Average percentage of activity budget for the whole group during Wet and Dry periods is shown in Figure 1. Statistically significant difference was found only in resting

behavior with individuals resting more in Wet than in Dry periods ($T_p = 3.9$, $p = 0.001$). While instantaneous samples underestimate rare or brief events such as aggression (Dunbar, 1976), analyses of all occurrences of agonistic behaviors per hour of observation confirm the suggestion that seasonal fluctuations in wild food abundance were unrelated to average agonistic interaction rates (wet: 1.07, dry: 1.08). In addition, the lack of a seasonal trend for changes in time spent foraging suggests that provisioning eliminated many potential seasonal effects on rates of energy acquisition.

Figure 2 about here

In both seasons, individuals started the day foraging with little time spent in social activities (Figure 2). During the period when food was distributed, there was a significant decrease in time spent foraging and significant increases in resting (Table 1). In the Dry season, when natural food availability was lower, grooming and agonistic interactions also significantly increased during the midday period relative to the morning and afternoon periods (Table 1).

Table 1 about here

While trade-offs among the time spent in different activities are expected, there was a positive relationship between time spent in foraging and agonistic interactions, and a negative one for foraging and all affiliative (grooming + social play) interactions. This relationship was especially marked during Dry periods (Forage and Agonistic: dry, $r_s = 0.55$, $p < 0.05$; Forage and Affiliative: dry, $r_s = -0.83$, $p < 0.01$; Forage and Affiliative: wet, $r_s = -0.62$, $p < 0.05$, $N = 18$).

Age-Sex Differences in Activities

Adult males and females did not differ in the percentage of time spent foraging, in locomotion or resting in either season. Adults, especially males, foraged significantly less but moved and rested significantly more than did juveniles in both seasons (Forage wet: $F_{2,18} = -2.5$, $p<0.01$, Forage dry: $F_{2,18} = -3.1$, $p<0.05$; Locomote wet: $F_{2,18} = 3.3$, $p<0.01$; Locomote dry: $F_{2,18} = 3.1$, $p<0.01$; Rest wet: $F_{2,18} = 4.1$, $p<0.01$; Rest dry: $F_{2,18} = 4.3$, $p<0.01$). Adult females were more involved in grooming interactions than were males and juveniles (significant only for Dry periods; $U = 12.6$, $p < 0.01$) while juveniles played significantly more than adults did in both seasons (Dry: $U = 11.3$ $p <0.01$; Wet $U = 13.9$, $p < 0.01$). No age or sex differences were found in the time spent in agonistic interactions.

Rank Differences in Activities

During the dry period, a significant negative correlation was found between individual dominance rank and time spent foraging ($r_{s18} = -0.54$, N= 18, $p<0.05$, partial correlation controlling for the effects of age) and between rank and locomotion ($r_{s18} = 0.74$, N= 18, $p<0.01$, partial correlation controlling for the effects of age) with dominant individuals spending more time foraging and less time in locomotion than did subordinates (note that hierarchy is numbered with higher ranking individuals having smaller numbers. Therefore, negative correlations means higher ranking doing more, and positive correlations mean higher ranking doing less). Other correlations between rank and behavior during the dry period and all correlations during the wet period were not significant.

Use of Space

The group made intensive use of the area with the most natural vegetation: $\chi^2_{dry} = 97.013$, $df = 2$, $p < 0.001$, $\chi^2_{wet} = 20.64$, $df = 2$, $p < 0.01$ (expected values based on approximate proportional size of each area: 1 = 1/18; 2 = 2/18 and 3 = 15/18 – table 2). During dry

periods of low natural food abundance, group members tended to spend more time in Area 1 (where food could be stolen), while in wet periods of higher abundance they used Area 3 most ($\chi^2 = 6.2$, df=2 p = 0.045). Group cohesion also varied seasonally. Proximity between group members decreased during drier periods and thus the group became less cohesive ($\chi^2 = 11.5$, df=1, $p<0.01$, Figure 3).

Table 2 and Figure 3 about here

DISCUSSION

General Activity Budgets

In spite of provisioning, the unconfined use of an 18ha area resulted in an activity budget very similar to that of wild groups of *Cebus* (Robinson, 1981; Rose, 1994) with a mean of *c.* 50% forage, 15% locomotion, 15% rest, and less than 2% for grooming, social play and agonistic interactions. Individuals started the day foraging for natural foods and finished the day foraging and playing. During the midday period of food distribution, agonistic and grooming interactions peaked, but only during the dry season.

This midday increase in agonistic interactions and grooming could have two explanations. Izawa (1980) described grooming among a wild provisioned group of *C. apella* as an activity occurring predominantly during resting periods. Thus it is possible that after eating, relaxed and satiated individuals engage in grooming before resting. A second possibility is that grooming was used to reduce tension among group members. Janson (1985; 1988) and di Bitetti (1997) observed that most grooming interactions in wild *C. apella* groups occurred during visits to larger fig fruit trees, and suggest that grooming serves as a mechanism to reduce aggression (e.g. Keverne *et al*., 1989) while feeding in

close proximity on a valued and clumped resource (Fruth & Hohmann, 2002). Furthermore, Phillips (1995b) describes increases in rates of aggression and of affiliative behavior between *C. capucinus* individuals during the use of clumped resources. Grooming during such times is suggested as being used to reduce tension and to facilitate coalitionary behavior between dyads in order to defend a feeding patch.

Effects of Provisioning

While Boinski *et al.*'s (2000) caveat about exploring functions of behavior in non-natural groups needs consideration, the development and refinement of socio-ecological models have been achieved in part as a result of studies conducted under such conditions (e.g. de Waal & Luttrell, 1986; Chapais, 1992, 1995). Moreover, many influential contributions to the understanding of the dynamics of coalitionary and grooming behaviors come from studies conducted on captive or semi-captive groups (e.g. de Waal, 1982; de Waal & Harcourt, 1992).

For the study group, provisioning probably accounted for the lack of seasonal differences in activity budgets of adults and relatively constant rates of agonistic interaction, although Ferreira *et al*. (2006) found that coalitions were more frequent during feeding contexts than during other activities. Provisioning was insufficient to meet the metabolic needs of all individuals in the group, but could be monopolised. As a result, there was an association between dominance rank and time spent foraging and in locomotion specifically during the dry season High ranking individuals were able to meet their daily metabolic requirements more easily, spending less time foraging and with a reduced need to travel through the area. Seasonality also affected the use of space and group cohesion. Daily opportunities for direct contest competition for preferred foods

were induced via the clumped nature of the provisioning while scramble competition could be inferred from changes in cohesiveness and use of different foraging areas during periods of lower natural food abundance, rather than through consistent differences in the allocation of time to different activities.

Characteristics of competition

Analyses show that both of our predictions were confirmed, and three characteristics of competition for resources (regarding direct competition, use of space and cohesiveness) can be proposed. Firstly, the individuals in this group actively competed for clumped (provisioned) resources. During food distribution, rates of aggressive behavior peaked (e.g. Figure 2), and this was especially marked during the dry season when natural foods were limited in availability. Increased rates of aggression during the use of preferred food sources have consistently been found for other *Cebus* groups (Janson, 1985; O'Brien, 1991; Izar, 1994, 2004; Rose, 1994; Perry, 1997). The mean rate of 0.9 agonistic events/hr observed here was higher than in other studies of *C. apella* (Izar, 1994; Janson, 1985), and of *C. capucinus* groups where rates of aggression vary between 0.86 - 0.72 events/hr (Phillips, 1995b).

A second characteristic of competition was the differential use of space from wet to dry periods. Fluctuations in the use of space suggest that seasonal variation in natural food availability influenced the competitive regime within the group, forcing individuals to adjust their foraging areas and thus altering their access to natural resources. We propose that these changes in the ways in which individuals forage through space reflect the outcome of scramble competition since no clumped wild foods that could be monopolized were detected (Ferreira, 2003).

A third aspect of food competition relates to the decrease in cohesiveness seen during periods of low food abundance, which we suggest acted to minimize both direct and scramble competition while foraging for insects or other embedded resources. This decrease in inter-individual proximity is again indicative of general spatial and behavioral mechanisms to reduce competition among group members, irrespective of its predominant mode.

Coalitionary behavior among female capuchins has been related to contest competition (see Perry, 1997; Vogel *et al.*, 2007). Unrelated females in this group did not form coalitions with each other or in support of offspring, and most of the coalitions observed were adult males supporting immatures (Ferreira *et al.*, 2006). However, most coalitions did occur during contests over food, with the alpha male as the intervener in rare disputes among adult females (Ferreira *et al.*, 2006). The lack of coalitions among females and of obvious nepotism is unlikely to be an artifact of the "experimental" conditions of the study site, since direct contests for food did occur, and provisioning did indeed provide opportunities for contests over resources as well as close proximity (e.g. Vogel & Janson, 2007). In addition, being low ranking in the group implied significant disadvantages to individuals in terms of time spent foraging or locomotion during the dry period, but not for other social behaviors, or for use of central and peripheral positions (Ferreira, 2003). While we have not directly assessed caloric intake rates by rank (e.g. Vogel, 2005), a lack of preponderant rank effects on activities again suggests that contest competition alone did not underlie the organization of the group.

In conclusion, we suggest that provisioning enables the assessment of the relative importance of modes of contest for social dynamics, and that the relative importance of each form of competition will vary as a function of changing internal group dynamics and variability in the nature and distribution of foods, whether natural or provisioned. Teasing

apart the combination of social and ecological opportunities for and constraints on modes of competition contributes to an understanding of how competition influences relationships within social groups of primates, and may contribute to refinement of socio-ecological models.

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Figure legends:

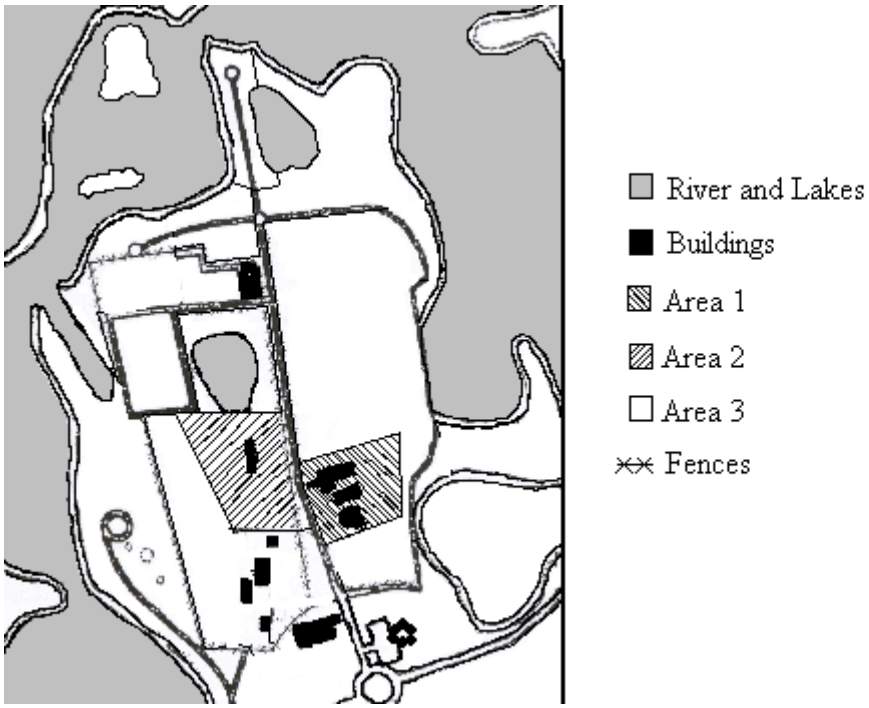
Figure 1. General view of the study area

Figure 2: Mean and SD activity budgets by time ad season. N= 18 individuals in each seasonal (Dry or Wet) and Time period (am, midday, pm.) Significant comparisons shown in table 1.

Figure 3: Cohesiveness of the group measured as the mean percentage of samples with either no neighbours or three or more neighbours within a 10m radius of the focal animals (N = 18) by wet and dry season.

1 Figure 1

2



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1 Figure 2a:

2

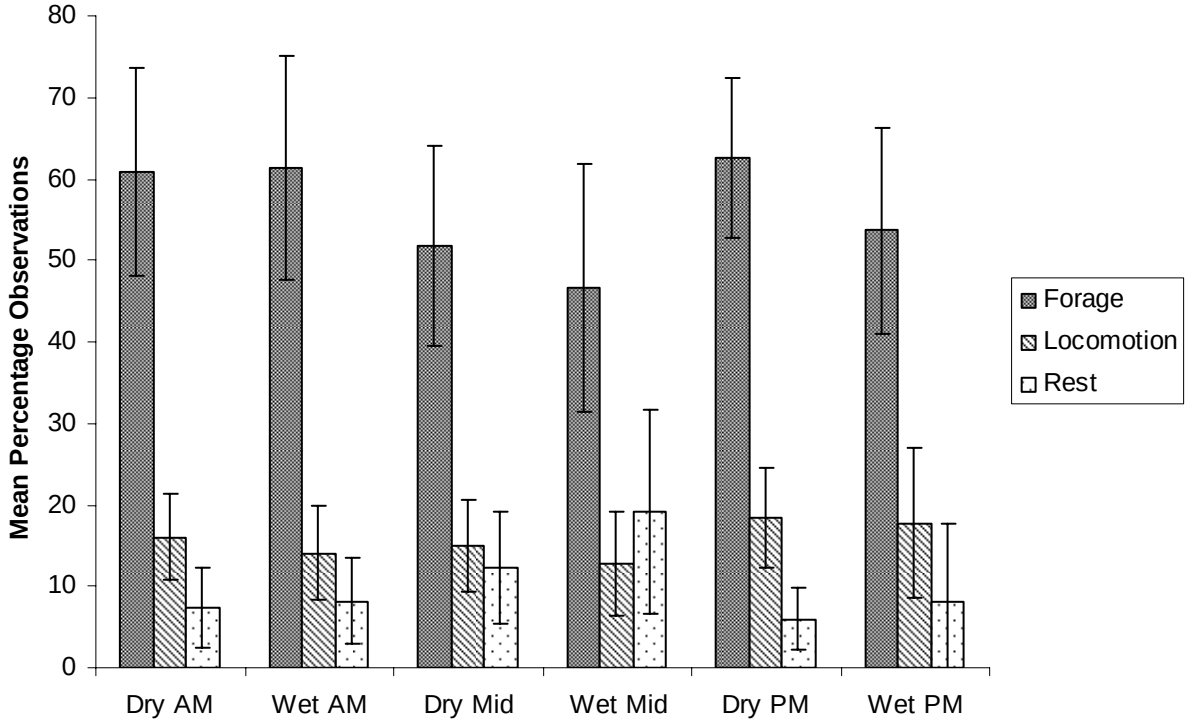

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Figure 2b

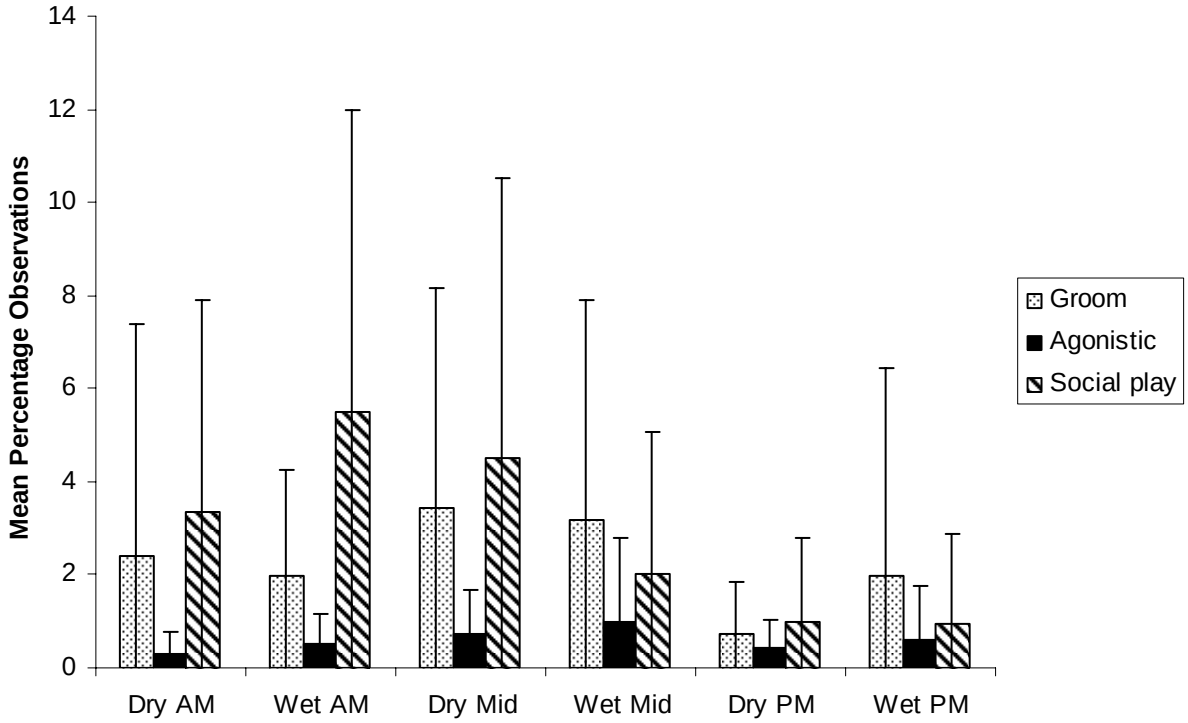
Mean Percentage Observations
14
12
10
8
6
4
2
0
Dry AM
Wet AM
Dry Mid
Wet Mid
Dry PM
Wet PM
Groom
Agonistic
Social play

Figure 3

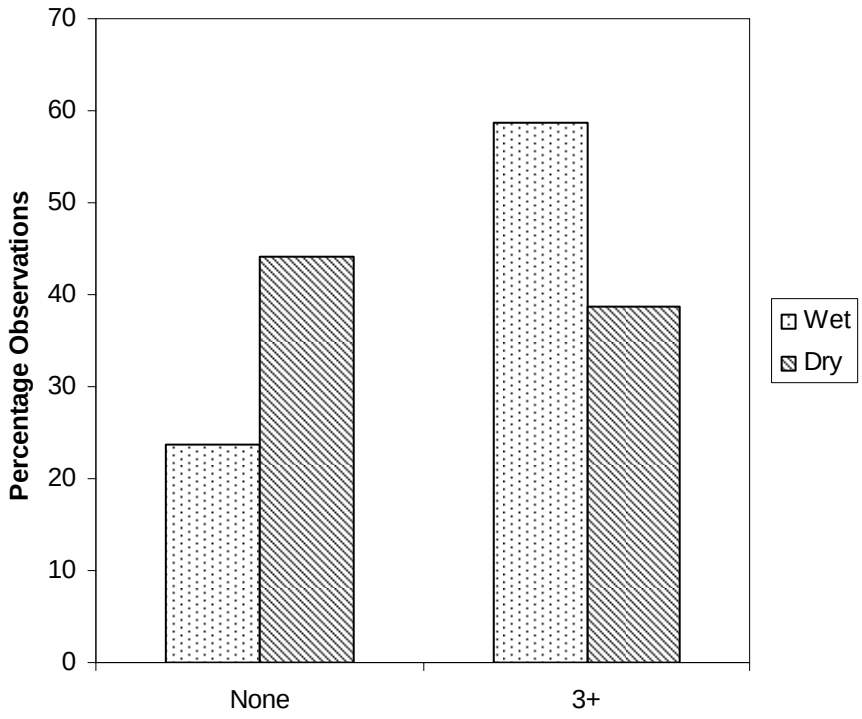

Table 1. Statistical comparison of time spent in different activities among the three time periods (Morning, Midday, Afternoon; all N = 52). Only significant comparisons are shown.

	Forage	***Locomotion***	***Rest***	***Groom***	***Aggression***	***Social Play***
Wet	F=5.073 $p < 0.01$ (post-hoc: m ≠ mid)	F=2.199 $p = 0.121$	F=6.074 $p < 0.001$ (post-hoc: m ≠ mid; mid≠a)	χ=3.176 $p = 0.204$	χ=4.36 $p = 0.113$	χ=8.667 $p = 0.13$
Dry	F=4.461 $p < 0.01$ (post-hoc: mid≠a)	F=1.844 $p = 0.169$	F=7.111 $p < 0.01$ (post-hoc: m ≠ mid; mid≠a)	χ=10.073 $p < 0.01$ (post-hoc: mid≠a)	χ=1.19 $p = 0.55$ (post-hoc: m ≠ mid; mid≠a)	χ=2.036 $p = 0.36$

M = morning period (06:00 to 10:59am); mid = 11:00 to 14:59; a = 15:00 to 19:00

Table 2: Frequency of use of the three areas in the two seasons

	Area 1 **(1.2 ha)**	**Area 2** **(1.5 ha)**	**Area 3** **(15.3 ha)**
Wet	14.5%	10.2%	75.3%
Dry	25.9%	15.7%	58.3%